

ETHOLOGY OF *CEROTAINIA ALBIPILOSA* CURRAN
(DIPTERA: ASILIDAE) IN MARYLAND:
COURTSHIP, MATING AND OVIPOSITION¹

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Abstract.—Male *Cerotainia albipilosa* (Curran) exhibit a complex aerial courtship in front of perched females. The position of the male in flight and subsequent behaviors are discussed. Most courtship flights by males fail to terminate in mating. Males mount females following a rear or frontal flight approach. Non-receptive females display agonistically toward courtship males. The mating position consists of male over female and lasts for an average 11.5 minutes. Unlike many asilid species, mating pairs do not fly *in copulo*. Females initiate separation of mating pairs. Most courtship flights and matings occur between 2:00 and 5:00 PM. The egg chorion is bright amber in color and oval in shape; one averaging 0.25 and 0.29 mm in width and length, respectively. Elevated ridges occur on the surface of the chorion except in the immediate area surrounding the micropyle.

Several workers have contributed significant information on the basic reproductive habits of asilid flies (Poulton, 1906; Melin, 1923; Richards, 1929; Bromley, 1933; Wilcox and Martin, 1936; Hull, 1942; Dennis and Lavigne, 1975, 1976; Lavallee, 1970; Lavigne, 1963, 1964, 1968, 1970a, 1970b, 1971, 1972; Lavigne and Dennis, 1975; Lavigne and Holland, 1969; Lavigne et al., 1976; Lehr, 1970; Musso, 1972; Alcock, 1977). Many of the asilid species reported in these studies displayed specific patterns of pre-mating behavior. For many species, premating behavior consisted of short rapid flights in which males searched for receptive females. Matings, following these flights, were initiated either in the air or on substrates. Those initiated in the air began when males overtook females in flight. Following a brief struggle, the pair fell to the substrate where copulation ensued. Those initiated on substrates began when a male landed on a perched female nearby. In the former, the male landed on the female's dorsum, faced the same direction as the female, clasped her genitalia, and assumed a copulation position. In the latter, the male quickly mounted the perched female from the side or rear. In both examples, a brief struggle sometimes preceded genital contact.

Courtship behavior has been observed in some species of at least eleven asilid genera (*Heteropogon*, *Promachus*, *Diogmites*, *Stichopogon*, *Holopogon*, *Dioctria*, *Stelidopogon*, *Cyrtopogon*, *Proctacanthella*, *Proctacanthus*, *Ablautus*). Courtship behavior involved a hover flight in most species, although leg extension was sometimes included when the male approached

a potential mate. Males of five species (*Cyrtopogon glarealis* Melander, *C. auratus* Cole, *C. montanus* Loew, *C. marginalis* Loew and *Ablautus rufotibialis* Back) performed courtship behavior, which also included leg extension, on substrates in front of perched females. Matings were initiated when males landed on the female's dorsum or mounted them from substrates.

Mating positions are usually 'tail to tail' or 'male over female' although some species may show slight modifications of either position.

Oviposition habits of females are variable, depending on specializations of their genitalia. In many species, the posterior segments of the abdomen are modified into slender structures for inserting eggs between and below substrates; in others a circlet of spines is present on the 9th abdominal tergite and is used for digging and covering eggs with soil. Still in other species, neither specialization is present; and presumably they drop their eggs in flight or place them on surfaces or inside fissures in plants or decaying wood.

Methods and Procedures

Extensive field observations of *Cerotainia albipilosa* Curran were made at the Loch Raven Watershed in Baltimore County, Maryland. General methods and procedures for observations made in the field were described earlier (Scarbrough and Norden, 1977). Field observations were recorded on tape and later transcribed into a notebook. Photographic records of various behaviors were taken whenever possible. A Yashica movie camera with a zoom lens was used to record complex behaviors such as courtship oscillations, attempted mountings and agonistic displays. The movies were analyzed to obtain a more accurate understanding of these behaviors.

Results and Discussion

Courtship and mating.—Courtship flights performed by *Cerotainia albipilosa* males involved aerial displays conducted in front of females resting on sunlit perches. Most courtship flights occurred in mid- to late afternoon (Scarbrough and Norden, 1977). At this time females selected perches which ranged from 5 cm to 6 m above ground. However most females (85.1%, $N = 2,151$) were concentrated on perches situated below 3 m.

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Figs. 1-4. 1. Typical positions of a male and female resting on a perch prior to a courtship flight. The female is at the tip of the leaf; 2. Typical posture of a non-receptive female following an attempted mounting by a male. Note the positions of the wings, hind legs and arched abdomen; 3. Typical mating position of *Cerotainia albipilosa*; 4. Egg of *Cerotainia albipilosa* (100 \times).



Males rested on and launched courtships from various plant perches located 1–6 cm behind and 1–2 cm above or below perched females. A male sometimes occupied the same perch on which the female rested (Fig. 1).

While enroute to the courtship position, the male usually flew several cm above or below the perched female to a position about 7–10 cm in front of her. Upon arriving at the latter position, he rotated his body 180° while hovering and faced the female. When the male's flight path was to one side of and at the level of the female, she invariably flew toward him as if he were potential prey, but she turned away before making contact with him. Both sexes usually returned to their perches before the male resumed courtship flights.

In the courtship position, male *C. albipilosa* employed hover flights with leg extensions when approaching a perched female. From this hover position, males oscillated slowly forward and rearward 3–7 cm in front of females before attempting to mount them. During the forward phase, the male's fore legs were elevated to the sides of its head and extended toward the female. The midlegs were directed below the body, and the hind legs extended ventrolaterally and formed an angle of 45–60° from the body. The male hesitated in the forward phase about 3 cm in front of the female and palpated his front tarsi. During the rearward phase, his fore legs dropped below his eyes, and mid- and hind legs remained in one of the previously described positions. The duration of an oscillation averaged 4 s but ranged from 1–12. The average number of oscillations per courtship flight was 5 but ranged from 1–9. Males usually rested on perches near females between courtship flights.

Frequently during an oscillation, a male quickly retreated backward to a position about 15 cm in front of the perched female and then darted forward touching the female's head, thorax and/or wing bases. However, in some cases the male stopped his forward progress just prior to reaching the female only to retreat again. He sometimes did this 2 or 3 times before touching the female. The male's mid- and hind legs were drawn up below his body when he touched the female with the extended fore tarsi. Darting flights were usually preceded by 2 or more forward oscillations and occurred prior to the male's attempt to mount a female.

During courtship, males of *Heteropogon* spp. (Lavigne and Holland, 1969; Lavigne, 1970b; Lehr, 1970; Alcock, 1977), *Cyrtopogon* spp. (Wilcox and Martin, 1936; Lavigne, 1970a; Lavalley, 1970), *Holopogon albipilosa* Curran (Dennis and Lavigne, 1975), *Ablautus rufotibialis* (Lavigne, 1972) and *Stichopogon trifasciatus* (Say) (Lavigne and Holland, 1969) approach prospective mates with leg extension in a similar manner as that performed by male *Cerotainia albipilosa*. With the exception of *C. willistoni* (Curran), males of the above species also move forward and touch females with their fore tarsi. The tarsi and tibiae of all legs of *C. albipilosa* are covered with

silvery-white hairs. Parts of the fore tarsi of males of the above species, with the exceptions of *Holopogon albipilosa* and *Stichopogon trifasciatus*, are ornamented with white hairs. Dorsal patches of white hairs are also on the middle tibiae of *Heteropogon maculinervis* James; and all legs of *Stichopogon trifasciatus* are pollinose, with short appressed silvery hairs. The position and movement of the ornamented fore and midlegs and subsequent contact of the female with the male's fore tarsi undoubtedly serve as visual and tactile stimuli which convey conspecific information to females (Lavallee, 1970; Lavigne and Holland, 1969; Alcock, 1977).

Males of *Heteropogon lautus* Loew (Bromley, 1933) and *Stichopogon trifasciatus* (Lavigne and Holland, 1969) include a lateral movement during the courtship hover. Soon after assuming a courtship position or following a rearward phase of an oscillation, *Cerotainia albipilosa* males hovered for about 1–5 s before resuming forward movements. At this stage they sometimes moved 1–2 cm to the right or left of the females. These lateral movements appeared to be primarily associated with sudden changes in wind speeds and shifts of their bodies produced by normal wing movements. Lateral movements were more apparent on windy than on calm days.

Non-receptive females of *C. albipilosa*, like *Heteropogon stonei* Wilcox (Alcock, 1977), responded to oscillating males by moving parts of their bodies singly or in combination and/or flying after males. As a male moved toward a female, she spread her wings laterally so that the wings formed an angle to her body of 50–60°; she frequently vibrated her wings and tilted her body forward. Her abdomen was sometimes vibrated up and down, although it was usually elevated and held in a stationary position above the perch at an angle of 30–40°. She sometimes extended her fore legs and 'waved' her tarsi in a boxing motion toward the male. When a male touched a female's dorsum, the female rocked forward, vibrated her wings and lowered her abdomen. If a male attempted to mount, a female elevated her wings and hind legs above her body and curved the tip of her abdomen down against the perch. She then vibrated her wings and kicked her hind legs at the male (Fig. 2). Females responded to lateral movements of males by pivoting on their midtarsi and shifting their bodies to face them. Frequently females flew from these crouched or tilted positions to chase males or to forage for prey. Females forage when they are non-receptive (Scarborough, 1978). It is assumed that these movements and subsequent postures of *Cerotainia albipilosa* females provided the primary means of communicating non-receptivity to males and, at the same time, placed them in the normal position from which to fly.

Males usually courted a single female for 20 or more minutes, but periods ranged from 0–204. Zero periods represent those instances when searching males were immediately chased away upon arriving at the site

by non-receptive females or other courting males. During this period a male often courted a female several times ($\bar{x} = 6/5$ min interval; $R = 1-10$) with brief interruptions for attempted mountings and perchings. While courtship flights took place during most of the diurnal activity period, most flights occurred from 2:00-5:00 PM. Air temperatures at courtship heights ranged from 22-34°C.

Searching *C. albipilosa* males sometimes appeared to court other Diptera and the ends of twigs. Other asilid species (*Holcocephala abdominalis* (Say), *H. clava* (Loew), *Holopogon phaenotus* (Loew)), syrphids (*Allograpta* spp.) and tephritids (*Rhagoletis* sp.) were abundant, occupied perches during the day near female *Cerotainia albipilosa*, and were courted frequently by males. Larger flies, such as *Musca domestica* L. (Muscidae) and *Sarcophaga* spp. (Sarcophagidae), were less abundant and were courted less frequently. Asilids and syrphids were alarmed by this attention, and males usually remained with and courted them from 1-2 min. The remaining dipterans were easily disturbed and flew away almost immediately. No mounting attempts were observed. Additionally, males frequently courted perched males of the same species, and on occasion, the ends of dead twigs. These courtships were brief, usually consisting of one or two oscillations. Thus it is assumed that searching males cannot recognize conspecifics until the proper responses are performed.

Most courtship flights by male *Cerotainia albipilosa* failed to terminate in matings. This is true of several asilid species exhibiting aerial displays (Lavigne and Holland, 1969; Lavigne, 1970a, 1970b; Dennis and Lavigne, 1975; Lehr, 1970). During over 400 hours of observing courting males, only 38 successful mountings and subsequent matings were observed. Mountings of females were accomplished from a frontal or rear approach. From a frontal approach, a male flew to the usual courting position in front of a perched female. He then flew directly to a position about 2 cm above her; and while hovering, he rotated his body 180° to be in line with hers. Upon landing, the male grasped her wings and abdomen with his legs. The end of his abdomen looped downward, between his legs and over the end of her abdomen. The male's claspers grasped the female's genitalia and union was accomplished. From a rear approach, a male flew directly from its perch behind the female, landed on her dorsum and grasped her in the above manner. Prior to both approaches, males courted females several times before attempting to mount them. When males were unsuccessful in mounting, they flew to perches behind females before resuming courtship flights.

Because of the limited number of complete matings (38) observed and the speed at which the observed ones occurred, it was not possible to ascertain what signal(s) was (were) emitted by the female to indicate acceptance. The only detectable response produced by females was the

elevation of the ends of their abdomens prior to union of the genitalia of the sexes. Perhaps receptivity is signaled indirectly by the absence of agonistic behavior toward males attempting to mount. Females which were totally non-receptive flew after and chased males away as soon as they assumed a courtship position. In other cases, females tolerated courting males for several minutes before chasing them away. One male oscillated 37 times in front of a female during a 15 min period (1:03–1:18 PM), while touching her only 6 times. The female appeared to ignore the male during much of the courting period (23 min), although sometimes she spread her wings and vibrated them and her abdomen when he approached her. She also foraged 3 times and fed on one prey during the courtship. The female chased him 4 times before he departed the area. In contrast, another male oscillated 42 times during a 15 min period (2:12–2:27 PM) while darting forward and touching the female 28 times. The female also foraged 5 times and fed on 2 prey during this period but displayed her wings only once and did not chase the male. The pair mated at 2:33 PM. Thus it seems plausible that non-receptivity in females exists at various levels and may be influenced with appropriate internal (satiation) and external (courting males) stimulation.

While mating pairs were observed from 12:06–5:10 PM, the majority (88%) took place between 2:00 and 5:00 PM. Most pairs were found on sunlit upper surfaces of perches at heights ranging from 30 cm up to about 7 m above ground. When temperatures exceeded 34°C pairs moved to the shaded margins of or below leaves. Air temperatures ranged from 25–38°C at heights where mating pairs were observed.

Males usually attempted to mount females from a frontal approach during courtship. Most of the successful (73.6%; $N = 38$) and unsuccessful (70.9%; $N = 2,261$) mountings were initiated following oscillations in front of females. The remaining successful (26.4%; $N = 38$) and unsuccessful (29.1%; $N = 2,261$) rear mountings were directed from perches and excluded an oscillatory or hover flight. In each case, the male courted the female for several minutes prior to perching and subsequent mounting or attempted mounting. Seven of the successful and 223 of the unsuccessful rear mountings occurred immediately after females returned to perches following various flight activities. Males which had been courting females followed them in flight and mounted or attempted to mount them as soon as they landed, without assuming a courtship position. If females were receptive and received appropriate stimulation, they allowed males to mount from either frontal or rear approach. However, the position assumed by courting males in front of a female probably functioned as an orientation mechanism for the sexes. Thus males were in an effective position from which to recognize conspecifics, to convey species specific information and to mount females.

Male courtship flights and female flight activities frequently attracted other males to the female's perch. It was not unusual to find 2 or 3 males simultaneously attempting to court a single female. This situation occurred several times when a single male courted a female for long periods (>25 min). These situations were brief since the resident male soon began to attack the intruders. The attacks consisted of two males meeting in midair and flying in a tight downward directed spiral. The flights usually terminated a few cm above the ground although a few pairs crashed into shrubs or high grass. Resident males sometimes rammed or grappled with intruders in air while falling to the ground. Physical damage to the flies was not detected. The males also produced a high-pitched, audible buzz during these encounters. The resident male usually remained in the area and courted the female.

Most mating pairs (95.9%; $N = 222$) of *C. albipilosa* took the 'male over female' position (Fig. 3), although a few pairs (4.1%; $N = 222$) were found clinging to margins of leaves or twigs in a chain position. In the latter position, both sexes were holding onto the perch, and their bodies formed variable angles, ranging from 55 – 95° .

Mating pairs remained at the original female perch sites until the sexes separated. The average duration of 38 complete matings was 11.5 minutes ($R = 10$ – 15). Partial mating durations of 184 pairs ranged from 5–18 minutes. Females usually initiated separation by slowly pushing alternately with their hind tarsi at the mounted males. Continued pushing eventually dislodged males from their dorsal positions. Still connected by their genitalia to females, males fell backward and assumed a head down position with their dorsal surfaces facing the same direction as the female's head. In this position females began to vigorously kick at males with both tarsi, simultaneously. The males responded by either immediately separating from the females in the suspended position or crawling to a position on a perch beside the females before separating. Times of normal separations (female leg kicking and genital disengagement) ranged from 6–20 seconds. In some cases males released females without the usual tarsal probing. Approach of a predator (*Vespula* sp.) was also sufficient to stimulate males to loosen their grasps of females and fly away.

Upon separation, members of a mating pair reinitiated behaviors which were interrupted by mating. Males usually flew from the area, although some remained and courted the same female or others nearby. Females sometimes flew to another perch, but they usually remained at the mating site where they foraged and fed and/or were courted again.

Females sometimes mated several times during the flight season. Marked females were observed at 15 min intervals/h from 2:00–5:00 PM during a 7 day period (11–18.VIII.76). These observations showed that of 40

marked females, 20% mated each day, 10% mated more than once per day and 5% were not observed mating. In one case a female mated with the same male twice. The male began to court the female immediately after the first meeting. He courted her for 16 min before mating the second time.

Unlike many asilid species, *Cerotainia albipilosa* does not fly while in copulo. Mating pairs rested on fully exposed sunlit perches in an almost motionless state. Movement was usually restricted to females' maintaining their positions on perches, discouraging intruders or probing at mounted males near the end of mating. Intruder males usually hovered in the courting position in front of mating pairs. Females responded by extending their fore legs and slowly waving their tarsi at the approaching intruders. The intruders then either flew away or landed near mating pairs on perches where they probed the tips of their abdomens toward the female's genitalia and apparently attempted to mate with them. Mating females responded by kicking at them with their hind legs and/or crawling to new positions on perches. Kicking by females and the inability of males to clasp their genitalia was usually sufficient to discourage the intruders. Continued probing by one or more intruding males sometimes induced separation of the mating pair. Similar reactions were elicited when a pair was touched with a pencil. Females waved or kicked their legs at the probing pencil and then crawled away. When captured in vials, mating pairs did not separate until they were vigorously shaken, and females moved only to maintain a balanced position. Mating males usually maintained a thanatosis-like state until they released their grasp on females. Mating males occasionally elevated their wings and vibrated them when exposed to these stimuli. This response appeared to be more a function of maintaining balance than an agonistic display.

According to some investigators (Cloudsley-Thompson, 1961; Poulton, 1906; Hobby, 1931; Musso, 1971), some asilid males may present potential mates with food before mating or court only feeding females. In each case females were momentarily engaged in feeding which permitted a period for males to mate with females and, at the same time, to escape predation from the latter. Evidence to support this suggestion is lacking (Dennis and Lavigne, 1975). Behavior patterns of *C. albipilosa* do not support this suggestion since 1) males court without prey (Scarborough, 1978), 2) males court both non-feeding and feeding females (only 40% ($N = 596$) of the courted females were feeding), 3) only 7% ($N = 212$) of the mating females were feeding and 4) cannibalism was not observed.

Eggs and oviposition.—Attempts to obtain eggs in the field and from live or decapitated adults placed in vials for oviposition were unsuccessful. Eggs were obtained by dissecting live females in Ringer's Insect Solution. Females to be dissected were taken at random throughout the flight season.

Eggs found in calyces, oviducts and connecting genital chambers were considered to be mature since their chorions were sclerotized and the darkest in color. The number of developed eggs obtained from 30 females ranged from 52–148 with most flies (17) having over 100. In addition, each ovary consisted of about 20 ovarioles which contained 5–8 developing eggs. Six females captured *in copulo* early in the season (5–10.VII.73) and dissected lacked mature eggs, but the ovarioles contained numerous oocytes. Although the number of eggs produced by a single female was not determined, these results indicate that 1) eggs are produced continuously during the female's life, 2) eggs are not mature and ready for fertilization when females emerge, but require a period for maturation and 3) females may mate before eggs are mature.

Sclerotized chorions of mature eggs were uniform in color, shape and size. They were bright amber, slightly oval and averaged 0.25 mm in width and 0.29 mm in length (100 eggs, 10 from 10♀♀) (Fig. 4). The chorion had characteristic elevated ridges forming 4–7-sided rings with 6-sided rings being the most common. Melin (1923) reported similar structures on eggs of *Laphria* spp. and *Dioctria* spp. At one end, the ridges faded away to form a smooth surface which surrounded the micropyle. Other microstructures associated with insect chorions were not visible at 550×

Oviposition habits of *Cerotainia albipilosa* females are unknown. Only one oviposition was observed during this study. A perched female (13.VII.74; 3:41 PM) lowered its abdomen, touched the tip to the perch and released 3 eggs consecutively. She groomed the tip of the abdomen with her hind legs and flew away. Air temperature at the oviposition site was 31°C. Other females (12) behaved similarly by touching the tips of their abdomens to perches and grooming their abdomens, but eggs were not located. The female's ovipositor is minute and lacks specialization for inserting eggs into substrates. Females of *Dioctria*, *Laphria* (Melin, 1923) and *Andrenosoma* (Musso, 1971), which also lack genital specializations, typically deposit eggs into holes or grooves on substrates or while in flight. Thus *Cerotainia albipilosa* females probably behave similarly by depositing eggs at perches or at specific sites among vegetation in the area where they forage and mate.

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Footnote

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